SOME LIMITING FACTORS AND RESEARCH NEEDS OF ENDANGERED HAWAIIAN FOREST BIRDS

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It is well known that Hawaiian birds are particularly susceptible to depopulation and extinction. Twenty-three of 69 endemic species or races have disappeared since discovery of Hawai'i by Europeans 200 years ago.

Except for Warner (1968) and Atkinson (1977), only superficial inquiries have been made into historical aspects and underlying factors of the Hawaiian forest bird decline. After several years of field and laboratory investigation, Warner explained the disappearance of forest birds as being caused primarily by disease. Atkinson advanced a theory based on historical evidence that arboreal predation by rats was a leading factor.

The object of my long-term historical investigation is to document and compare the salient facts on the geography and chronology of Hawaiian bird loss, species by species; to chronicle what is known about all factors of depopulation--predation, disease, habitat alteration, and food competition; and to draw such conclusions as seem warranted.

At the First Conference in Natural Sciences two years ago, Banko and Banko (1976) reported on the potential significance of food depletion in the decline of Hawaiian forest birds. The role played by the Big-headed ant (Pheidole megacephala) in destroying much of the endemic insect fauna at elevations generally less than 3000 feet (914 m) before 1890 was sketched at that time. (The term "insect" will be used hereafter as including other arthropods as well).

I now wish to elaborate on the possible impact of foreign parasitic flies and wasps in depleting native insect foods important to the small Hawaiian forest birds at higher elevations. It is acknowledged at the outset that all of the information in the historical literature dealing with habitat alteration, predation, disease, and food competition as they relate to bird decline, has not yet been fully extracted or analyzed. However, the effects of habitat destruction are in evidence almost everywhere around us, while claims that disease and predation were leading factors in bird depopulation are now being systematically studied by Charles van Riper and James K. Baker, respectively. It may

therefore be of interest to review some historical facts indicating parasitism of bird food-insects by foreign flies and wasps played a prominent role in depopulating birds through depletion of food supplies. If this theory is correct, foreign parasites may be a major factor limiting population size and range of forest birds today.

In considering the significance of insect foods to forest birds, it is first necessary to point out that insects are important, if not essential, in the diets of the young of all species, irregardless of food preferences of adults. Though specific foods of nestling and newly-fledged forest birds have not been studied extensively, judging from what has been recorded in the literature, their diets appear to consist principally if not entirely of insects.

The history of events in a forest ecosystem above 3000 feet (914 m) elevation illustrates the destructive impact of foreign parasites on native insect foods and indirectly on populations of endemic forest birds, thereby serving as a model of typical effects which have occurred in Hawaiian National Parks and elsewhere. A suitable case history is provided by the Acacia koa forest which extends some 40 miles (64 km) along the Kona Coast, at approximately 4000 to 7000 feet (1219-2134 m) elevation.

Eighty-five years ago this Kona Koa forest supported substantial populations of the 'Oma'o (Phaeornis obscurus obscurus), 'O'u (Psittirostra psittacea), and Greater Koa Finch (Psittirostra palmeri), to mention but a few of the dozon or so species of small forest birds which formed the avifauna of that particular region. Perkins (1903: 375, 433, 437) noted the 'Oma'o to be "almost ubiquitous throughout the forest . . . . from the lower limits to the upper"; the 'O'u in Kona "in countless numbers," moving seasonally upwards into the Koa woods; and the Greater Koa Finch seen in "hundreds" between 4000 and 5000 feet (1219 and 1524 m) in the Koa belt.

Today, judging from a review of the literature and from personal observation, populations of the 'Oma'o, 'O'u, and Greater Koa Finch are either absent or in low numbers in the Kona Koa forest, exemplifying what has happened to other native Hawaiian forest birds in Kona and elsewhere.

Consider the following ecological relationships and history of events. Acacia koa, especially old decadent stands, is of paramount importance to Hawaiian forest birds as a source of insect food. Beginning in 1887 a long procession of naturalists and ornithologists found more kinds of birds in Koa woods than in any other type of Hawaiian forest. In retrospect, the most obvious rationale for avian diversity in Koa forests is that Acacia koa harbored a greater variety of endemic insects than any other generic group of Hawaiian trees (Swezey 1954: 1).

Of all the insects hosted by Acacia koa none were apparently as important as food to more kinds of forest birds than the endemic moth genus Scotorythra spp. (Geometridae). After years of observing feeding behavior and investigating stomach contents of many species of Hawaiian forest birds, Perkins (1913: clii) concluded that Scotorythra spp. "form a most important part of the food supply of endemic birds, and are supplied by the parents to the young of nearly all the species, while they are a favorite food of many adult birds as well." The historical record is replete with references to the prominence of Scotorythra spp., and other caterpillars, in diets of Hawaiian forest birds.

While Scotorythra spp. moths and larvae were found on Hawaiian trees and shrubs other than Koa, it was the species that fed on Koa that were in such demand. Some species of Scotorythra hosted by Koa were very abundant in the 1890's, and occasionally erupted, defoliating entire forests.

In Kona, the 'Oma'o, 'O'u, and Greater Koa Finch had special affinities for Scotorythra spp., or looper caterpillars as they were commonly called. Perkins (1903: 374) mentions several instances of the 'Oma'o feeding on Koa loopers and adds that these birds "also continue to feed the young on these for some time after they have left the nest." Perkins (1903: 433-434) also documented the seasonal dependence of 'O'u on caterpillars after fruiting of its normal food, 'Ie'ie (Freycinetia arborea), had terminated. On several occasions, Perkins observed excursions of the 'O'u out of its usual haunts into Koa woods for the purpose of obtaining (Scotorythra spp.) caterpillars. Likewise, Perkins (1903: 437) noted that the Greater Koa Finch displayed an affinity for Koa looper caterpillars.

Unfortunately, Scotorythra caterpillars are also preyed upon by foreign parasitic insects which began arriving in the Islands about 1890 and continued to become established until at least 1942. While the impact of foreign organisms on insect foods of native birds has never been systematically studied in the field, at least four kinds of exotic flies and wasps are known to attack Scotorythra spp. What little is known of the arrival and status of foreign parasites in the Islands, and their relationships to Scotorythra spp., is condensed in Tables 1 and 2.

According to various authorities quoted in Table 1, two foreign tachinid flies arrived before 1900 and, one at least, was universal in mountain forests about 1892. An ichneumonid wasp was first discovered on O'ahu in 1925 and by 1931 had become very numerous at times. A braconid wasp was introduced in 1942 and not long thereafter was found well into the native forests of the six major Hawaiian Islands. Some foreign fly and wasp parasites apparently have high reproduction and dispersal characteristics.

By the 1940's it was known from impromptu investigations by authorities cited in Table 1, that the two tachinid flies attacked one and three species of Scotorythra spp., respectively. The ichneumonid wasp was discovered to hit seven species of Scotorythra spp., four host-specific to Acacia koa. The braconid

wasp was found to parasitize the larvae of one species of Scotorythra spp. moth hosted by Acacia koa.

Most, if not all of the prey-parasite relationships cited by E. C. Zimmerman in Table 2 were discovered by an economic entomologist, O. H. Swezey. During a long life of work in the field and laboratory, from about 1904 to the late 1930's, Swezey spent what time could be spared from his official duties in the forest studying Hawaiian insects.

In the 40 years since Swezey ceased to be active in the field, other potential parasites of Scotorythra spp. have arrived, creating a need for revision and possible expansion of host relationships shown in Table 2. For example, Bianchi (1959: 993) documented the introduction to Hawai'i of three braconid wasps, including Apanteles marginiventris and Meteorus laphygmae, in addition to the apparently accidental arrival of another tachinid fly, Eucelatoria armigera. Bianchi reported that it was not long after arrival of these parasites in 1942 that they became abundant in the lowlands and then spread to the upland grass ranges and even well into native forests where he theorized they might parasitize native caterpillars unrecorded as hosts. Whitesell (1964) stated, from a forester's viewpoint, that Scotorythra spp. appeared to be under good control biologically and seldom built up to "damaging levels."

Reduction of Scotorythra spp. populations by continental flies and wasps is not the only example which might be cited of depletion of a valuable insect food by foreign parasites. Another large group of endemic moths extensively parasitized by foreign insects is the family Pyralidae. Pyralids were major foods of the Palila (Psittirostra bailleui) and Greater Koa Finch (Psittirostra palmeri), and a general food of the Hawaii Creeper (Loxops maculatus mana), according to Perkins (1903: 436, 437; 1913: clx). In Kona, Perkins (1903: 414, 435) found the Hawaii Creeper "extremely common" at about 3500 feet (1067 m) upwards, and the Palila "extremely numerous" from below 4000 to at least 6000 feet (1219-1829 m).

Commenting on the biological control of species in one genus of Pyraustidae, Hedylepta, Zimmerman (1958b[8]: 66, 68-69) states:

> . . . eight foreign wasps and three foreign flies are extremely active parasites, and parasitism now commonly exceeds 90 per cent . . . Two of the species of this genus (Hedylepta) break the general rule that endemic Hawaiian insects are not pests of economic importance, because (H.) accepta is the well-known sugarcane leaf-roller, and (H.) blackburni is the common coconut leaf-roller. The introduction of parasites to control these species, especially the sugarcane leafroller, have resulted in mass destruction of the endemic Lepidoptera and have greatly altered the composition of the insect fauna of the islands.

Today the Palila is not known to inhabit the Mamane (Sophora chrysophylla) zone of the Kona Koa forest and the Hawaii Creeper appears to be much less common than in the past.

Foreign flies and wasps were not the only organisms depleting foods of forest birds. Other continental and Hawaiian organisms also compete with endemic forest birds for food. But continental parasites appear to have played a dominant role in many areas.

It is clear from the historical record that endemic Lepidoptera were the most heavily utilized food resources of the small Hawaiian forest birds in the 1890's. Concerning their general depletion in the past 80 years, Zimmerman (1958a[7]: 28) has this to say:

> When Dr. Swezey laid down his pen and left Hawaii (in 1952) a golden era of Hawaiian entomology closed . . . Swezey was the last of the entomologists to have seen many of the endemic Hawaiian Lepidoptera in a semblance of their natural abundance. The importation of parasites to control various moths of economic importance, together with the accidental importation of other parasites has resulted in wholesale slaughter and near or complete extermination of countless species. It is now impossible to see the Hawaiian Lepidoptera in the natural proliferation of species and individuals of Perkins day. Many are lost forever.

From an analysis of the historical literature, it may therefore be argued that depletion of insect foods by waves of foreign parasites was a significant factor in depopulation of endemic Hawaiian forest birds. If true, such a theory would have serious contemporary implications. Many continental ants, flies, wasps, and other foreign organisms are well established in native forests, and others continue to arrive. Wherever endemic birds are constrained to share food with continental fauna, superior competition by foreign species possess perhaps overlooked potential to significantly restrict population sizes and ranges of Hawaiian birds.

It is my contention that the overall predicament of endangered forest birds is primarily the result of dissolution of the natural Hawaiian ecosystem by continental fauna, and that the challenge of preserving what remains can best be accomplished by efforts to learn more about, maintain, and reestablish long neglected but vital interdependencies. Viewed in this light, research to determine the role of food supply in first reducing and then limiting population size of endemic Hawaiian forest birds is seen as an urgent conservation necessity.

In line with this thinking, immediate inquiry is needed to shed light on the following questions:

1. What is the present distributional relationships between availability of insect foods and endemic forest bird populations, especially during and after the critical nesting and fledging periods?

2. What proportions of diets of the various forest bird species are composed of foods of foreign origin?

3. Are foreign organisms limiting the quantity and quality of food presently available to forest birds? If so, which exotics are the most influential and where are they exerting the most competitive pressure?

4. Are Scotorythra spp. populations under biological control by foreign organisms as has been asserted?

5. What is the contemporary role of predatory ants in reducing food supplies of forest birds?

These and many other high priority questions face contemporary research ecologists charged with preserving endangered birds and maintaining native Hawaiian ecosystems.

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TABLE 1. Arrival and status of foreign parasites of *Scotorythra* spp. in Hawai'i.

TACHINID FLIES			
Chaetogaedia monticola	universal in mountain forests about 1892	still generally distributed over the Archipelago in 1931	Perkins (1913: clxxxiv, clxxxv) Williams (1931: 291)
Frontina archippivora	probably introduced in 1898	very common in Hawai'i	Williams (1931: 292)
ICHNEUMONID WASP			
Hyposoter exiguae	first discovered on O'ahu in 1925	at times very numerous	Williams (1931: 268-269)
BRACONID WASP			
Apanteles marginiventris	introduced in 1942	well into the native forest of 6 forested islands	Beardsley (1961: 364) Bianchi (1959: 993-994)

TABLE 2. Foreign parasites of Scotorythra spp. (Zimmerman 1958a[7]: 42-147).